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Effect of litter on soil respiration in a man-made *Populus* L. forest in a dune-meadow transitional region in China's Horqin sandy land

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ABSTRACT

Human disturbance and climate change both influence the input quantity of plant litter, significantly affecting soil respiration (R_s). However, what leads to a change of relationship between R_s in on-litter input (R_s(NL)) and natural litter input (R_s(CL)) is not yet fully understood. This study selected a man-made *Populus* forest in a dune-meadow transitional region to observe R_s(NL) and R_s(CL), soil temperature and soil moisture at a depth of 0–10 cm, groundwater depth between April and October in 2014 and 2015, and diurnal variations were carried out during the early, middle, and late stages of the growing seasons. Complex R_s diurnal patterns were observed in different growth stages. The soil moisture beyond field capacity inhibited root respiration and soil microbial activities, thus making R_s(NL) smaller than R_s(CL). When soil moisture was below field capacity with the increase of groundwater depth, dry air and low litter moisture content resulted in the shielding effect of the litter on R_s beyond its decomposition, thus making R_s(NL) consistently larger than R_s(CL). The temperature sensitivity was significantly affected by soil moisture. These results indicate that interactions among the quantity of litter, soil temperature, soil moisture and groundwater, which cause diurnal variations in R_s were diverse. Negative litter respiration may not be a measurement error, but caused by soil moisture which changes the relationship between R_s(NL) and R_s(CL). Thus, this study shows that plant litter has a significant influence on R_s in the dune-meadow transitional region. The findings of this study will provide useful information to understand these fragile ecosystems and the terrestrial carbon cycle.

1. Introduction

Soil respiration (R_s) is an important part of the terrestrial carbon cycle, returning approximately 80 PgC to the atmosphere each year (Raich et al., 2002). R_s is composed of three major carbon flux sources, namely root respiration and the release of CO_2 through microbial decomposition in plant litter and in soil organic matter (Kuzyakov, 2006). Among these, the decomposition of litter is responsible for around 68 Gt of CO_2 every year, accounting for about 70% of the annual carbon flux (Raich and Schlesinger, 1992). Most previous research into the effect of litter on R_s has focused on ecosystems in humid and semi-humid regions of the world (Deng et al., 2007; Fang et al., 2015; Rey et al., 2002), although recently some researchers have begun to turn their attention to arid and semi-arid regions (Zhang et al., 2014, 2016). Plant litter on the surface plays an important role in controlling soil erosion, determining nutrient cycling and ecological improvement (Luyssaert et al., 2007). It also contributes to the accumulation of soil organic carbon through microbial decomposition and humification (Palviainen et al., 2004), thus playing a key role in the construction of ecosystems. At the global scale, arid and semi-arid lands, which account for nearly one-third of the global land area, often suffer from poor soil and serious desertification (Reynolds, 2000); R_s is the main process responsible for carbon emission in these regions (Conant et al., 2000). However, as of now there are few studies of the impact of litter changes on R_s in sandy arid-semiarid regions where the ecosystem structure is particularly fragile.

Litter is the main carbon cycle pathway linking vegetation with the soil in forest ecosystems. Changes in the quantity and quality of litter on the ground therefore have an important influence on the release of surface CO_2 flux (Norby et al., 2001). Rises in CO_2 concentrations and atmospheric temperature, as well as changes in precipitation patterns, affect the quality and quantity of litter (Clark et al., 2010; Ellsworth

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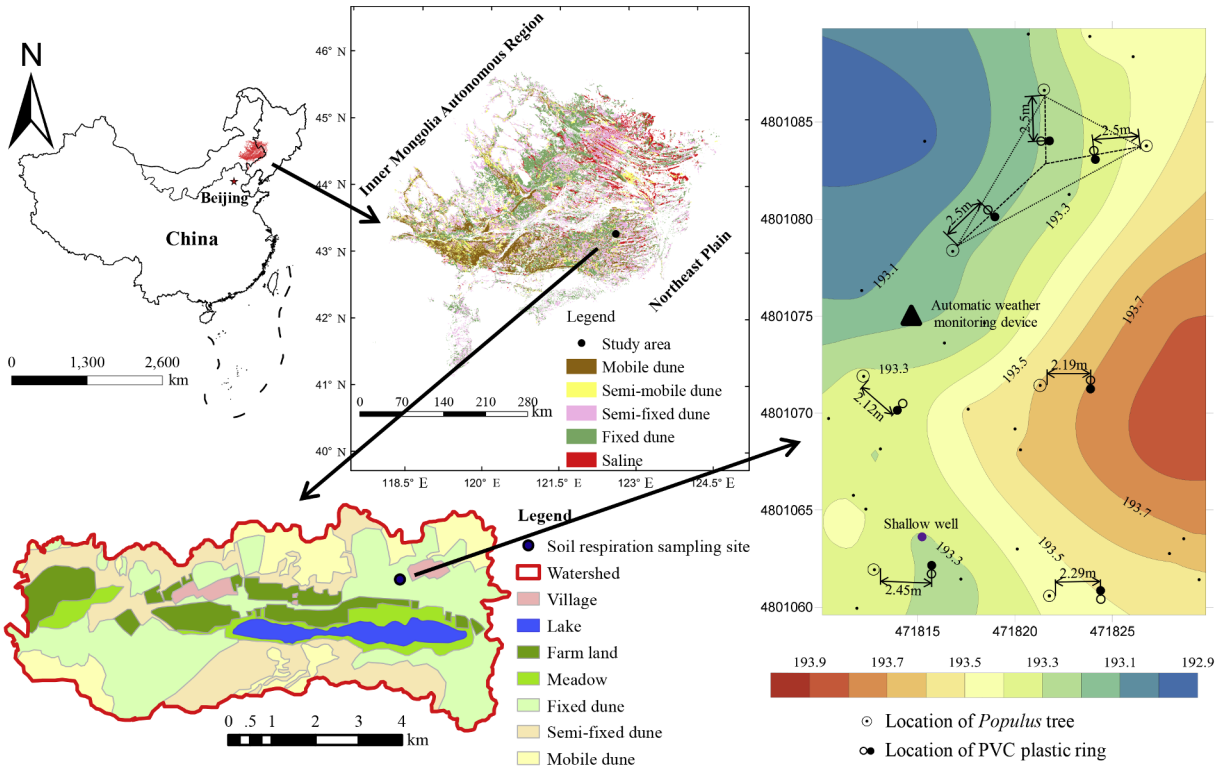

Fig. 1. Geographic location of the study region, the experimental area and the layout of the experimental plots.

et al., 2015), which in turn affects R_s. Litter removal reduces the decomposition of soil organic carbon by decreasing the easily decomposable substrate for microbes (Wang et al., 2013). Increased litter inputs trigger priming effects, thus increasing soil CO_2 emissions in temperate forests (Crow et al., 2009; Sulzman et al., 2005). A number of studies have verified that the removal of litter significantly reduced R_s (Raich and Nadelhoffer, 1989; Wu et al., 2017; Yan et al., 2013) and the addition of litter increased CO_2 flux (Fang et al., 2015; Schaefer et al., 2009). In addition, increased litter boosts R_s in natural forests but not in plantation forests, which may be related to its lower soil fertility and its high clay content in plantation forests (Liu et al., 2017). However, Berryman et al. (2014) and Zhang et al. (2014, 2016) found that the litter respiration (R_L) was negative under normal and double litter conditions, and suggested that this which might have resulted from high variability in respiration rates relative to a low treatment effect, or that it might indirectly reflect the response of R_s to soil moisture. Based on the above analysis, the management of litter in different regions appears to vary somewhat, with a consequent impact on its effect on R_s. However, so far very little research has been done to try to explain what causes negative R_L. If negative R_L is found in tests, it is usually considered a measurement error and ignored. This view can seriously affect the accuracy of the prediction of terrestrial carbon emissions.

Soil temperature (T_s) and soil moisture (M_s) are the most important factors affecting R_s, explaining most of the variation observed in R_s (Borken et al., 2002; Fang and Moncrieff, 2001). The contribution of aboveground litter to R_s also largely depends on T_s and M_s (Fekete et al., 2014). However, the response of R_s on T_s can be altered under both very high and very low M_s (Londo et al., 1999; Welsch and Hornberger, 2004). The Horqin Sandy Land is the largest sandy land in China, and desertification is the most serious. It experiences relatively low levels of precipitation and the primary water sources of vegetation and soil water are mainly from groundwater. Under these conditions, meadows, fixed sand dunes, and mobile sand dunes radiate out successively from the available water sources (e.g., rivers or lakes), forming a dune-meadow alternative distribution pattern, namely a dune-meadow cascade ecosystem. In the transition zone, the groundwater depth changes greatly with the growth period, thus pointing to the obvious influence on the surface M_s. Therefore, the transitional artificial poplar forest in the dune-meadow cascade ecosystem was chosen as the location for this study. The purpose of this paper is thus (1) to show the diurnal and seasonal changes in the characteristics of R_s in both soils covering litter and those with no litter (R_s(CL) and R_s(NL), respectively) in arid and semi-arid desertification regions; (2) to explore the influence of litter on R_s; and (3) to discuss the individual and interactive impacts of T_s and M_s on seasonal variations in R_s.

2. Materials and methods

2.1. Description of the study area

The study region is located in Agulazhen, Horqin Zuoyi Houqi Banner, Tongliao City, in the Inner Mongolia Autonomous Region in the northeast of China. The geographical coordinates of this region, which covers a land area of 55 km^2, are 122°33′00″–122°41′00″E and 43°18′48″–43°21′24″N. This region lies at the southeast edge of the Horqin Sandy Land. Its highest elevation is 235 m and its lowest 184 m. Sand dunes, farmlands, meadows, and lakes are distributed across the study area, which is a typical dune-meadow alternating region. The multi-year average precipitation is 389 mm, with rainfall mainly between June and September. The multi-year average water-surface evaporation, measured with 20 cm evaporation dishes, is 1412 mm, mostly between April and September with the greatest evaporation occurring in May. The annual average relative humidity is 55.8%, and the annual average temperature is 6.6 °C, with the highest monthly average temperature of 23.8 °C occurring in July. The annual average wind speed is 3–4 m/s, with the lowest wind speed between July and September. The vegetation communities in the region are simple, and the species diversity is low. The main plants in the region comprise *Artemisia halodendron Turcz. et Bess.*, *Phragmites communis Trin.*, *Salix gordejevii Chang et SkV.*, *Caragana microphylla*, and *Populus* L. Plants

Table 1
Base information for the *Populus* forest in the study area.

Year	SOM/g·kg^{-1}	TN/g·kg^{-1}	TP/g·kg^{-1}	TK/g·kg^{-1}	pH	EC/μS·cm^{-1}	FRB/kg.m^{-3}	FC/%	Humus horizon/cm	Litter/g·m^{-2}	
										Undecomposed	decomposed
2014	3.06	1.49	0.091	22.83	8.0	65.32	1.12 (2.1–2.5 m)	–	3.2–5.6	518.3	154.3
2015	3.69	1.41	0.097	22.15	8.1	68.08	1.76 (2–2.5 m)	15.86	6.3–9.5	826.1	489.2

mainly rely on natural precipitation to grow, although some of the wetland vegetation in the meadow relies on groundwater. Zonal and non-zonal soils are both present with an interlacing distribution across the study region; sandy, loam, sandy loam soil and loamy sand textures are the main soil types. The study region and the layout of the experimental sampling points are shown in Fig. 1.

A dune-meadow transitional region with a man-made *Populus* L. forest planted over fixed dunes with gentle slopes was selected for this study. A survey of the vegetation in the selected sampling squares indicated that the trees in the forest were 22–28 years old, with an average age of 25 years. The average tree height was 11.9 m and the average diameter at chest height 11.2 cm. The *Populus* distribution in the forest is shown in Fig. 1. Other low trees and herbaceous plants are distributed across the forest, primarily consisting of *Groussonetia papyrifera*, *Prunus padus*, *Artemisia selengensis turcz ex bess*, *Incarvillea sinensis*, and *Conyza Canadensis cronq.*, with a total coverage of approximately 20%. The ground elevation in the study area is between 193.0 m and 193.9 m and the soil type is loamy sand. The soil physiochemical properties and other relevant information for the sampling squares are shown in Table 1.

After the experiment, soil samples were collected from depths of 0–10 cm using a 100 cm^2 cutting ring at three points near the PVC rings in the plots (described in the next section). Soil organic matter (SOM), total nitrogen (TN), total phosphorus (TP), total potassium (TK), pH, electrical conductivity (EC) and field capacity (FC) were calculated. Litter from an area 1 × 1 m around each of the PVC rings was collected, sorted, dried at 80 °C and weighed. In the first year of the study, 2014, roots were collected from a 50 cm (length) × 50 cm (width) × 20 cm (depth) region around the PVC rings, cleaned, dried at 80 °C and weighed. In the second year, 2015, with the trunk base as the origin, the surrounding area was divided into three equal parts and one of the three selected. Roots in the 1–20 cm and 20–40 cm soil layers were collected from three areas (0–0.5 m, 1–1.5 m and 2–2.5 m out from the trunk base) and sorted by root diameter (less than 5, 5–10, 10–15, 15–20, and over 20 mm), and subsequently cleaned, dried at 80 °C and weighed. Fine root biomass (FRB) is all root biomass of the root diameter less than 5 mm in 0–20 cm soil layer. The data presented in Table 1 are the mean values of these parameters.

2.2. Experimental design

We installed automatic weather monitoring devices (Campbell) in the *Populus* forest and selected experimental plots near the automatic weather monitoring locations (Fig. 1). In 2014, four R_s measurement points were chosen along the south side of the plot, with the distance between each measurement point and the nearest poplar tree ranging from 2.1 to 2.5 m. In 2015, three adjacent poplar trees were selected. In each of the three directions radiating outward from the center of the triangle formed by the trees, an R_s measurement point was established 2.3 m from the poplar tree roots, for a total of three measurement points. In both years, a pair of homemade PVC plastic rings (inner diameter 10 cm, 7 cm tall, 5 mm thick) were installed alongside one another at each measurement point, with all the undecomposed and semi-decomposed litter inside the ring being removed in one member of the pair but left undisturbed in the other. The average thickness of the litter layer was 1.6 cm in 2014 and 2.2 cm in 2015.

2.3. Measurement methods

An LI-6400 portable gas analysis system (Li-Cor Inc., NE, USA) and an LI-6400-09 R_s chamber were used to measure R_s at each measurement point on 2–3 days each month during May–September 2014 and April–October 2015. Daily measurements were taken every 2 h during daylight hours (8:00–18:00) and care was taken to ensure that the plastic rings were undisturbed throughout each year's measurement period. Any green vegetation was cut off just above ground level 24 h before each measurement. On each measurement day, a portable soil moisture measurement instrument (Diviner2000, Sentek, Australia) and a soil thermocouple probe in an LI-6400 were used to measure M_s and T_s in on-litter input (M_s(NL), T_s(NL)) and natural litter input (M_s(CL), T_s(CL)), at a depth of 0–10 cm at each measurement point. Twenty-four hour continuous measurements were collected on August 20th (mid stage growth) and October 2nd (late stage growth) in 2014, and in April 29th (early stage growth), July 12th (mid stage growth) and October 2nd (late stage growth) in 2015.

2.4. Data processing and analysis

The exponential model established to describe the relationship between R_s and T_s is as follows (Lloyd and Taylor, 1994):

$$R_s = \alpha e^{\beta T_s} \quad (1)$$

where R_s is the mean soil respiration (μ mol m^{-2} s^{-1}), T_s is the mean soil temperature (°C), and α and β are constants.

Q_{10}, the temperature sensitivity index for R_s, refers to the ratio between the value of R_s at a given temperature to its value at a temperature 10 °C lower than the given temperature. Q_{10} is generally determined as follows (Boone et al., 1998):

$$Q_{10} = e^{10\beta} \quad (2)$$

When the relationship between M_s and R_s contains an inflection point, the following quadratic relationship is established:

$$R_s = \alpha M_s^2 + \beta M_s + \gamma \quad (3)$$

This leads to the following exponential-exponential relationship between R_s and T_s with M_s:

$$R_s = \alpha e^{\beta T_s} e^{(\gamma M_s + \delta M_s^2)} \quad (4)$$

where M_s is the mean soil moisture content (v/v %), and α, β, γ and δ are constants.

Berryman et al. (2014) and Zhang et al. (2014) suggested that the relationship between R_s(CL) and R_s(NL) is likely to suffer from high variability in respiration rates, either due to a low treatment effect, the inhibitory effect of litter on the respiration rate, or the intrinsic heterogeneity within the plots, all of which would result in a negative value for litter respiration. In this study, the standard deviations for measurements with 3 or 4 repetitions were small and the diurnal and seasonal variation patterns for R_s(CL) and R_s(NL) were the same, indicating that the factors that make R_s(CL) smaller than R_s(NL) are relatively stable in the study area. Considering the three reasons mentioned above by Berryman et al. (2014) and Zhang et al. (2014), it was the shielding effect of the litter they observed which was consistent with that observed in this study.

The difference observed between R_s(CL) and R_s(NL) in the current study is due to the difference in the amount of CO_2 released by litter decomposition and the amount of CO_2 shielded by the litter, which we refer to as the Δ litter respiration (ΔR_s(L)):

$$\Delta R_s(\mathrm{L}) = R_s(\mathrm{CL}) - R_s(\mathrm{NL}) \quad (5)$$

The litter contribution rate for R_s is:

$$C = \Delta R_s(\mathrm{L})/R_s(C\mathrm{L}) \quad (6)$$

where R_s(CL) is the control litter R_s, that is, the soil respiration in the ring containing the undisturbed litter, R_s(NL) is the soil respiration in the ring where the litter has been removed ($\mu mol\, m^{-2}\, s^{-1}$), and C is the contribution rate (%).

SPSS 19.0 was used for the statistical analysis and Excel 2010 to construct the figures and tables used to display the results. Analysis of variance (ANOVA) was used to analyze the significance of the difference between seasonal variation of R_s(CL) and R_s(NL) in the study area forest.

3. Results

3.1. Dynamic variation of environment

Fig. 2 shows the dynamic variations in the precipitation, T_s, M_s, and groundwater depth during the two-year measurement period. From May 1st to October 15th in 2014 and from April 1st to October 15th in 2015, the total precipitation was 307.7 mm and 363.6 mm, respectively. The daily average T_s showed a significant seasonal variation, with ranges of variation being 5.28 °C–22.70 °C (CL) and 6.51 °C–22.99 °C (NL) in 2014, and −0.10 °C to 21.74 °C (CL) and 1.65 °C–22.31 °C (NL) in 2015, with the average values being 16.58 °C and 17.18 °C in 2014, and 14.40 °C and 15.06 °C in 2015. The daily average M_s indicated a decreasing trend and the daily mean groundwater depth an increasing trend for both years. At the local level, both M_s and groundwater were significantly affected by precipitation. The ranges of variation for daily average M_s were 9.49%–22.06% (CL) and 7.97%–18.53% (NL) in 2014, and 11.43%–23.82% (CL) and 10.04%–20.45% (NL) in 2015, with the average values being 13.99% and 11.75% in 2014, and 17.56% and 15.21% in 2015. The ranges of variation for daily average groundwater depth were 0.71 m–1.42 m in 2014 and 0.43 m–1.25 m in 2015, with the average values being 1.11 m and 0.91 m, respectively. While the difference between T_s(CL) and T_s(NL) was non-significant ($P > 0.05$), that between M_s(CL) and M_s(NL) was significant ($P < 0.05$).

3.2. Dynamic variation of R_s

Seasonal variations of R_s in the man-made *Populus* forest first increased and then decreased in both 2014 and 2015, accompanied by relatively consistent variations in T_s (Fig. 2). Between R_s(CL) and R_s(NL) showed a significant correlation ($P < 0.01$) in each year. In 2014, R_s(NL) was larger than R_s(CL) during the growing season, with average values of 7.75 and 5.82 $\mu mol\, m^{-2}\, s^{-1}$, respectively; the average ΔR_s(L) was −1.93 $\mu mol\, m^{-2}\, s^{-1}$, and the average contribution rate of ΔR_s(L) was −35.82%. However, there was a completely different relationship between R_s(NL) and R_s(CL) in the early and late growth seasons of 2015. From April 12th to July 1st 2015 R_s(CL) was larger than R_s(NL), the average R_s values were 3.53(NL) and 8.17(CL), the average ΔR_s (L) were 4.64 $\mu mol\, m^{-2}\, s^{-1}$, and the average contribution rates for ΔR_s(L) were 57.79%. From July 12th to October 12th 2015 R_s(NL) was larger than R_s(CL), the average R_s values were 9.75(NL) 8.75(CL) $\mu mol\, m^{-2}\, s^{-1}$, the average ΔR_s(L) were −0.998 $\mu mol\, m^{-2}\, s^{-1}$, and the average contribution rates for ΔR_s(L) were −23.02% (Fig. S1).

The diurnal patterns of R_s(CL) and R_s(NL) were inconsistent in the early, middle and late growth stages in the man-made poplar forest (Fig. 3), including hysteresis on July 12th and August 16th in 2015 (Fig. 3*e and f*) and a multi-peak profile on August 20th and October 2nd in 2014 and April 29th and October 2nd in 2015 (Fig. 3*a–d*), with the maximum and minimum R_s occurring at different times. T_s diurnal variation showed unimodal distribution in different periods, and the amplitude of the M_s diurnal variation remained small throughout the study period.

3.3. Relationship of R_s with T_s and M_s

As shown in Fig. 4, the exponential relationship between R_s and T_s exhibited a significant positive correlation in both 2014 and 2015, with Q_{10} values of 2.6 (NL) and 2.97 (CL), and 4.97 (NL) and 3.11 (CL), respectively. R_s had a significant quadratic relationship with M_s except for R_s(CL) with M_s(CL) in 2015. The highest M_s values, which were most favourable for R_s, were obtained at 15.04% (NL) and 15.32% (CL) in 2014, and 14.12% (NL) and 16.86% (CL) in 2015. The results obtained for the two study years were slightly different, probably due to the changes in the measurement point locations and environmental factors, but all were close to the field capacity of 15.86%.

A bivariate fit using T_s and M_s showed different degrees of improvement compared to the single-factor model when interpreting R_s ($P < 0.01$) (Table 2).

4. Discussion

4.1. Effect of litter on soil respiration, soil temperature and soil moisture

T_s and M_s regulate R_s, while the cover of litter also causes the changes of T_s and M_s. The non-significant ($P > 0.05$) relationship between T_s(CL) and T_s(NL) and the significant ($P < 0.05$) relationship between M_s(CL) and M_s(NL) ($P < 0.05$) found in this study, echo the finding of Zhao et al. (2016). Furthermore, Nouvellon et al. (2012) pointed out that the decomposition of litter is rarely dependent on T_s changes, while M_s is known to be an important factor regulating the decomposition of litter (Fekete et al., 2014). However, Yan et al. (2013) showed that litter exclusion had no significant effect on T_s and M_s in three forest types. Xu et al. (2013) conducted a meta-analysis of 70 litter-manipulation experiments and revealed that litter manipulation had a significant impact upon T_s and M_s in forests, whereas the fluctuations of T_s and M_s in grassland were more intense. This is because different forest canopies intercept solar radiation by the branches and foliage differently (Lowman and Schowalter, 2012).

Although the selected R_s measurement points were very close, the experimental design and R_s measurement methods were the same, and the thickness of litter remained unchanged (1.6 cm in 2014 and 2.2 cm in 2015) across the measurement period in 2014 and 2015, the relationship between the size of R_s(CL) and R_s(NL) was not consistent. A more detailed analysis of the data revealed that M_s(NL) recorded on R_s observation days from April 12th to July 1st in 2015 were all above the field capacity of 15.86%, but M_s(NL) on R_s observation days from July 12th to October 12th and throughout the growing season in 2014 were consistently below this value (Fig. 2). Due to the effect of soil capillary force, the upward movement of groundwater the first affects root, and then gradually spreads to the surface soil. According to the soil moisture characteristic curve (Fig. 5), the 0–10 cm M_s (NL) reached the field capacity of 15.86% when the groundwater depth was 0.81 m. That is to say, when groundwater depth is below 0.81 m, M_s is larger than field capacity because it is affected by groundwater. It has been known for some time that when the main source of M_s is groundwater, groundwater is especially important for controlling R_s (Glenn et al., 1993). Based on the above analysis, it can be concluded that when the groundwater depth was less than 0.81 m, M_s(NL) was greater than the field capacity, and R_s(CL) was greater than R_s(NL) and that when the groundwater depth was over 0.81 m, M_s(NL) was less than the field capacity, and R_s(CL) was less than R_s(NL).

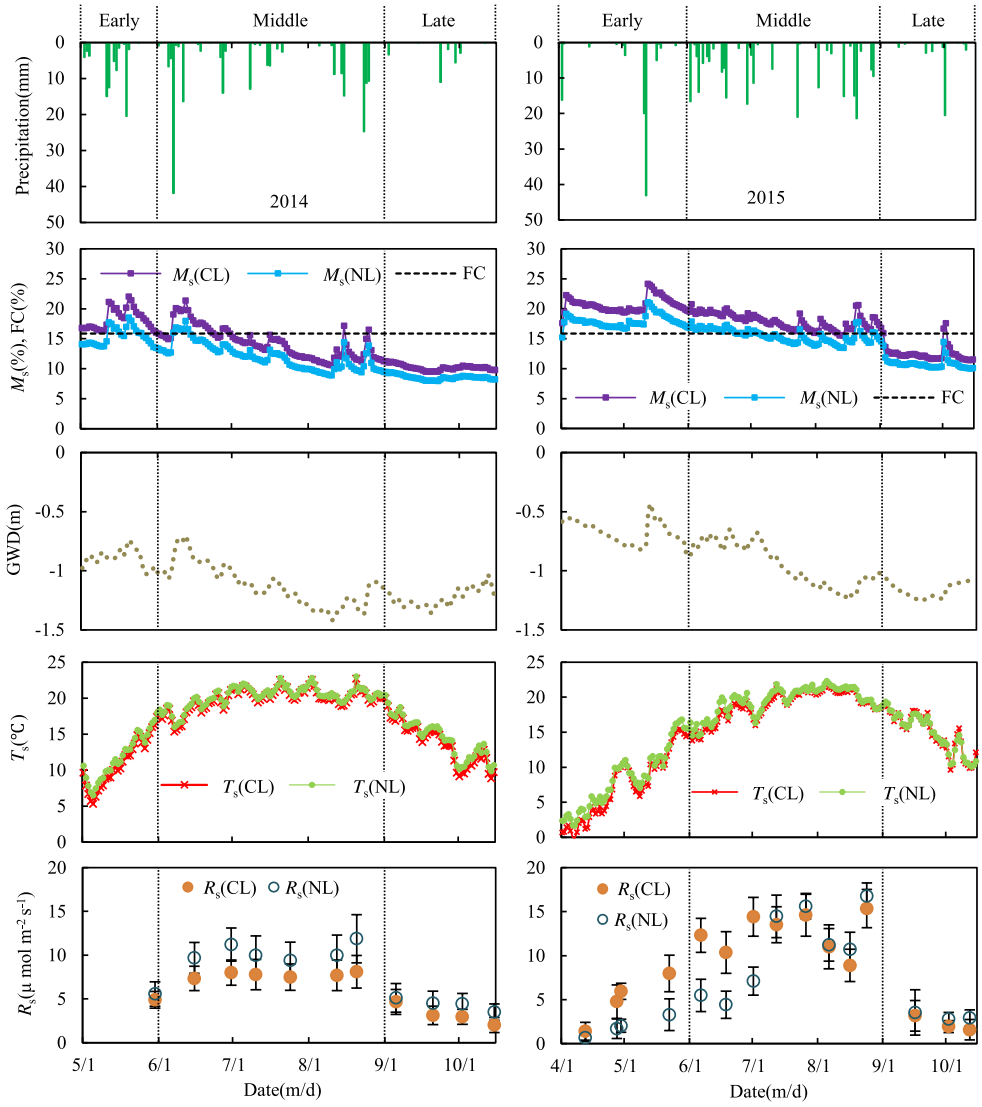

Fig. 2. Dynamic variation of soil respiration (R_s), soil temperature (T_s), soil moisture (M_s), precipitation and groundwater depth (GWD) during the 2014 and 2015 growing seasons (Precipitation was measured at 10 min intervals throughout the day (0:00–24:00, n = 144); the 0–10 cm volume M_s (cm^3 H_2O/cm^3 soil), the GWD (m), and the 0–10 cm T_s (°C) were recorded every 10 min throughout the day (from 0:00–24:00, n = 144); R_s was measured every 2 h during the day (8:00–18:00, n = 6) each year throughout the growing period).

The SOM content was low in the study area, but there was a 3.2–9.5 cm layer of humus on the surface due to the long-term accumulation of litter, which is the main source of soil organic matter (Sulzman et al., 2005; Wang et al., 2009). A previous study has found that the capillary root mass had a linear relationship with R_s (Pregitzer et al., 2000). In our study the roots in the vicinity of 2–2.5 m of the tree trunks were mainly distributed vertically in the 0–20 cm soil layer, accounting for 64.6% of the total root volume. Among these, the roots less than 5 mm in diameter accounted for 59.5% of the total in the study area (Fig. S2). Therefore, the main sources of R_s are root respiration and the CO_2 released by the decomposition of microorganisms in the litter and humus in the study area. The overall temporal patterns of R_s were found to be dependent largely on the relative proportions of the different components in total R_s (Chen et al., 2010). When the groundwater depth was less than 0.81 m, M_s (NL) was greater than the field capacity according to the soil moisture characteristic curve in this study. Higher M_s reduces the pore oxygen content and restricts the aerobic microbial metabolic activity (Oikawa et al., 2014; Skopp et al., 1990), thus reducing the rates of decomposition of CO_2 and microbial production (Linn and Doran, 1984), as well as filling the soil pores and hindering gas transmission (Moldrup et al., 2001, 2000). In this study, the roots respiration and the aerobic microbial metabolic activity in soil were restricted, and the CO_2 released difficultly from soil to atmosphere. The CO_2 released be by the decomposition of microorganisms in the litter was the major source of R_s, thus making R_s(CL) greater than R_s(NL). When groundwater depth dropped below 0.81 m, M_s(NL) was less than the field capacity according to the soil moisture characteristic curve, falling to a level that instead favored root respiration and microbial decomposition in the humus. However, due to the dry air in the study area, the litter and soil moisture after rain is evaporated rapidly. As litter moisture content and relative air humidity decreased, litter respiration became weaker (Berryman et al., 2014; Kuehn et al., 2004). In addition, due to the drop in M_s, the amount of water available to the litter also decreased. Here, the shielding effect of litter on the release of CO_2 from the soil was greater than that generated by its decomposition, causing R_s(CL) to be less than R_s(NL). The results of the experiments obtained by Berryman et al. (2014) and Zhang et al. (2016) showed that about 20% of the all measurements led to negative litter respiration. They attributed this phenomenon to variability in respiration rates, either due to a low treatment effect, the inhibitory effect of litter on the

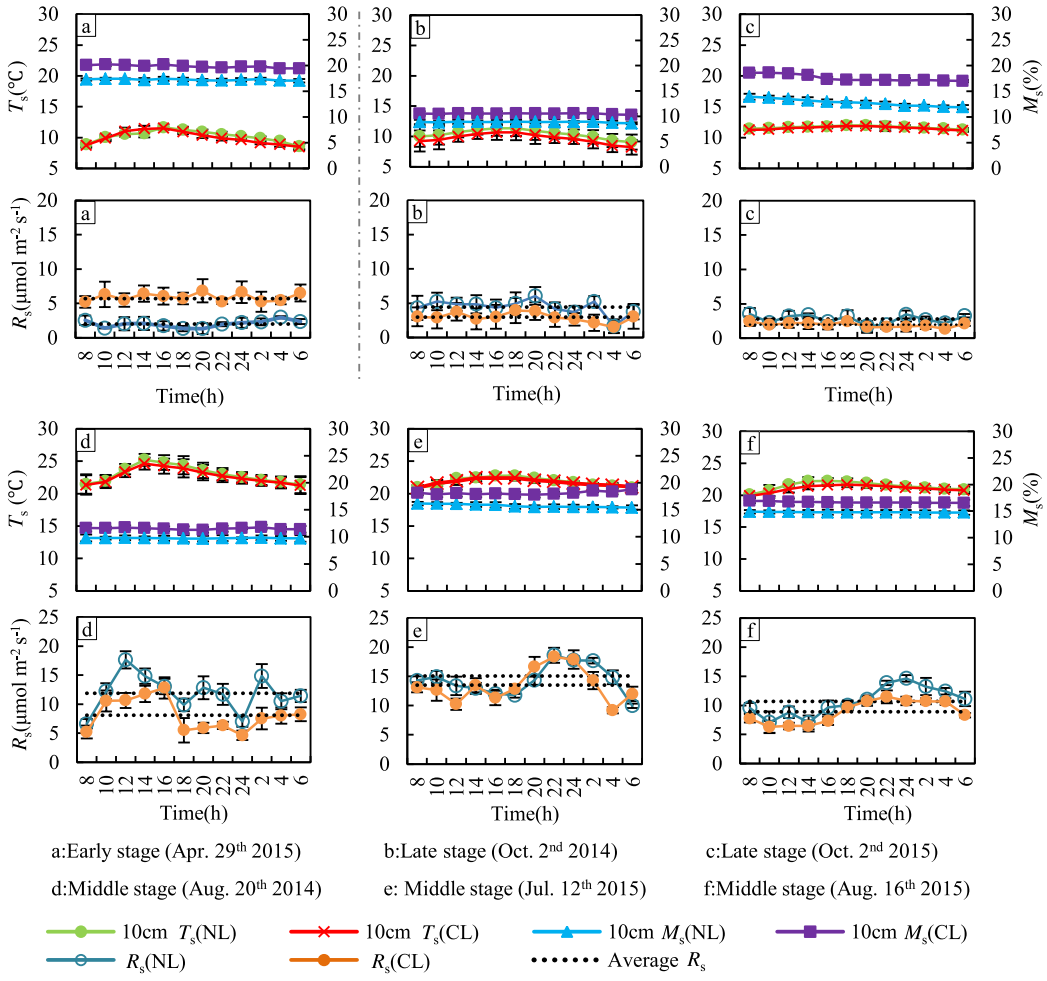

Fig. 3. Diurnal variation of soil respiration (R_s), soil temperature (T_s) and soil moisture (M_s) during the early, middle and late growth stages (In this study, the early stage is April and May, the middle stage is from June to August, and the late stage is September and October. Data are means that correspond to the number of R_s measurement points in 2014 and 2015).

respiration rate, or the intrinsic heterogeneity within the plots. Based on the above analysis, the negative litter respiration may not be a measurement error, but due to the fact that surface M_s is controlled by the groundwater. This process causes the changes in the different component proportions of R_s.

Rayment and Jarvis (2000) has argued that a change in T_s observed for a single day could be a key factor influencing and controlling the diurnal variation of R_s. The diurnal variation of R_s is known to be single-peaked and to have a significant exponential relationship with T_s (Wang et al., 2014). However, Yemadje et al. (2015) noted that although the variation of M_s within a single day is in itself insignificant, the fact that M_s governs the microbial activity indirectly affects R_s. Feng et al. (2014) has shown that there is a lag between R_s and T_s, and the lag time decreases as M_s increases. The diurnal variation of R_s in the man-made *Populus* forest observed in this study was more diverse (Fig. 3). The higher canopy of the man-made *Populus* forest increases vertical transport distances and thus has an impact on the lag time between maximum R_s and maximum photosynthetic active radiation, which results in a significant lag in R_s relative to T_s (Vargas et al., 2011). Litter regulates T_s and M_s by increasing soil infiltration of water and reducing surface runoff and evaporation (Adekalu et al., 2007). The 3.2–9.5 cm humus layer and the litter cover on the soil surface make the soil structure particularly complicated in the study area. The responses of decomposers are different in soils and litter (Manzoni et al., 2012). The decomposition of surface litter depends mainly on moisture, while the decomposition of soil organic matter is more closely dependent on temperature (Chen et al., 2010). Groundwater and rainfall also interfere with the effects of T_s and M_s on microbial activity. The complex soil structure and alternating effects of these various environmental factors lead not only to an indeterminate daily pattern in R_s, but also to inconsistences in the diurnal changes of R_s(CL) and R_s(NL).

4.2. Response of soil respiration to soil temperature and soil moisture

T_s can predict changes in R_s except when there are severe drought conditions, and the exponential relationship between them is now widely used and commonly applied to simulate Q_{10} of R_s (Lloyd and Taylor, 1994; Noh et al., 2017). This study identified a significant exponential relationship between R_s and T_s, and the Q_{10} values it found are consistent with the range for Q_{10} (1.10–5.18) generally found in Chinese forests (Xu et al., 2015). Litters have plasticity and serve a buffer function for soil (Deng et al., 2007). The result for 2014 indicated that removing litter reduced the Q_{10}, which is consistent with the conclusion that Q_{10} is proportional to the availability of substrate (Yang et al., 2011). The removal of litter exposed soil directly to the air, stimulating the evaporation of M_s and thus reducing the activity of decomposers (Sulzman et al., 2005). In the samples Q_{10}(CL) was fairly consistent across the two years. However, Q_{10}(NL) was significantly larger in 2015 than in 2014, and 2015 showed that removing litter increased the Q_{10}. This is likely because Q_{10} is not only affected by T_s, but also under the control of M_s (Boone et al., 1998). Due to the effect of groundwater in this study, M_s in the earlier stage of growth was greater

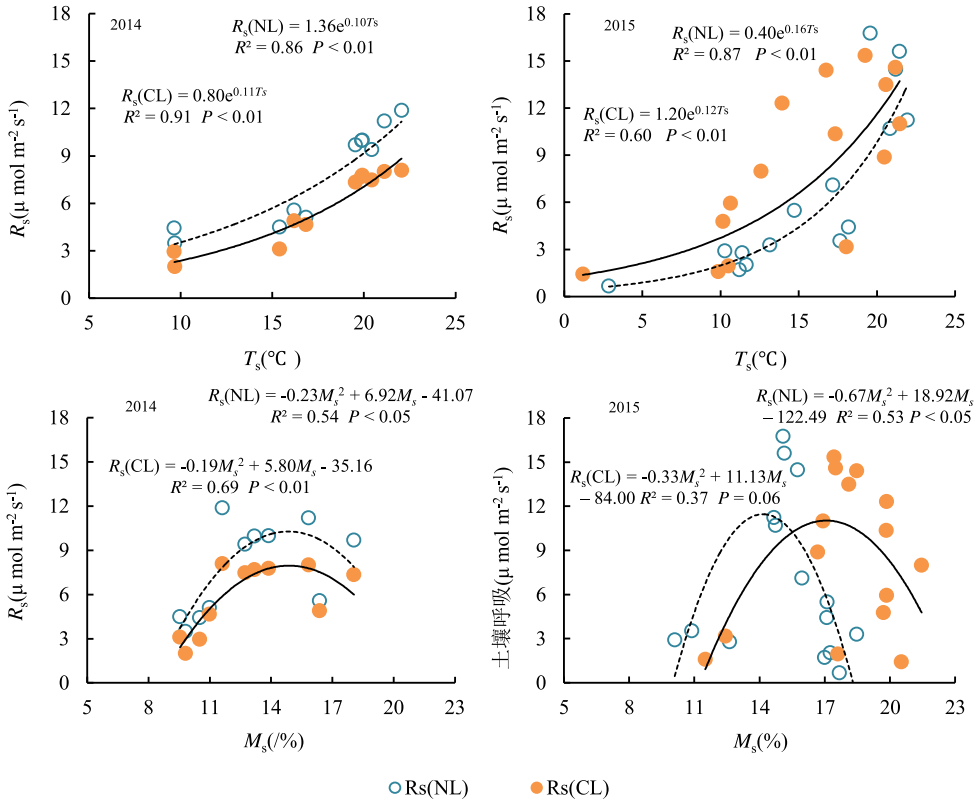

Fig. 4. Single-factor model for soil respiration (R_s) and soil temperature (T_s), soil respiration (R_s) and soil moisture (M_s) during the growing season (The dotted line and the solid line are the fitted curve with on litter and controlled litter, respectively. Date are means of value observed every 2 h from 8:00 to 18:00 in a day; n = 6).

than field capacity. The removal of litter stimulated the evaporation of M_s and increased oxygen content in soil, both of which were conducive to root respiration and microbial activity. Thus, the removal of litter favored the response of R_s(NL) on T_s. For a later stage of growth, M_s was less than field capacity. The dry litter contributed to a small portion of the total R_s and prevented the release of CO_2 from the soil. Thus, the control of litter reduced the response of R_s(CL) on T_s. Combinational effects of all factors during the growing season lead to Q_{10}(NL) being higher than Q_{10}(CL) in 2015. Zhang et al. (2013) found that in the North China Plain the autotrophic respiration for the wheat and maize growing seasons were more sensitive to temperature changes than heterotrophic respiration. The individual and combinational effects of biotic and abiotic factors may result in difference in the Q_{10} values of heterotrophic respiration and autotrophic respiration (Boone et al., 1998; Chen et al., 2017).

M_s had no discernible influence on heterotrophic respiration when it was between wilting point and field capacity, and became a controlling factor only at very high and very low moisture levels (Lellei-Kovács et al., 2011; Zhang et al., 2013). The relationship between R_s and M_s is more complicated, with linear (Davidson et al., 1998), quadratic (Sotta et al., 2004), exponential (Davidson et al., 2000), and logarithmic (Feng et al., 2014) curves, among others, being proposed. Our results indicated that M_s was primarily controlled by groundwater, with M_s ranging from 7.97% to 22.06% in 2014 and from 10.04% to 23.82% in 2015, and larger M_s inhibiting R_s, Thus R_s and M_s exhibited a quadratic relationship. The threshold values of M_s most favorable for R_s were close to the field capacity of 15.86% in 2014 and 2015, which is similar to Zhang et al. (2013). Moyano et al. (2013) also found that the optimal moisture potential value of microbial respiration was close to field capacity, and that R_s decreased as the soil water potential either increased or decreased away from this value. This further confirms that the field capacity represents a boundary that determines the impact of M_s on the relationship between R_s(CL) and R_s(NL).

The temporal variation in R_s and the contribution of aboveground litter to R_s are mainly influenced by T_s and M_s (Davidson et al., 1998; Fuentes et al., 2014). T_s and M_s often co-vary and jointly affect R_s (Epron et al., 2009). Due to the influence of the shallow groundwater depth, M_s was larger than the field capacity in the early stage of poplar growth from May to June (Fig. 2), with a consequent inhibitory effect on R_s. Meanwhile, T_s was low, microbial activity and root respiration were both weak, and R_s was also small. With the growth of vegetation and the increase of T_s, the groundwater depth increased and M_s

Table 2
Bivariate fitted model for the relationship between R_s, T_s and M_s during the growing season.

Year	Treat	Model	Factor	$R_s = \alpha e^{\beta T_s} e^{(\gamma M_s + \delta {M_s}^2)}$				R^2	P
				α	β	γ	δ		
2014	NL	Exponential- Exponential	T_s&M_s	0.214 (1.77)	0.078 (0.02)	0.303 (0.29)	−0.01 (0.01)	0.885	**
	CL		T_s&M_s	0.043 (1.10)	0.081 (0.01)	0.476 (0.18)	−0.02 (0.01)	0.964	**
2015	NL		T_s&M_s	0.014 (2.49)	0.130 (0.02)	0.522 (0.36)	−0.017 (0.01)	0.918	**
	CL		T_s&M_s	45.435 (7.73)	0.155 (0.03)	−0.766 (0.96)	0.028 (0.03)	0.846	**

** Significant at the 0.01 probability level.

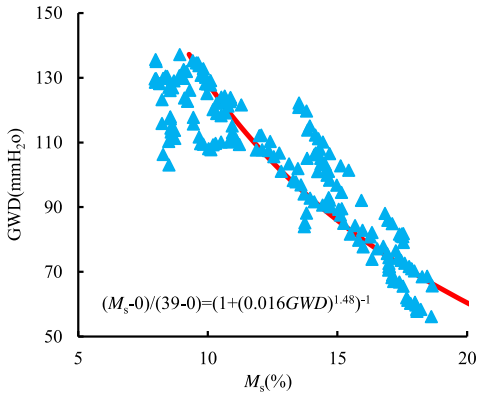

Fig. 5. Integrated soil moisture characteristic curve for soil moisture (M_s) and groundwater depth (GWD) in 2014–2015 during periods with no rainfall. (Excluded are the data on M_s and GWD on the days when it rained and the two days following during the 2014 and 2015 study period and applying the van Genuchten model ($\frac{M_S-\theta_r}{\theta_s-\theta_r} = [1 + (\alpha GWD)^n]^{-1}$ ($GWD > 0$), where M_s is the soil moisture (%), θ_r is the soil residual water content (%), θ_s is the soil saturated water content (%), GWD is the groundwater depth (m), α is the reciprocal of the soil intake value (1/m), and n is the soil pore size distribution index, the two-year integrated soil moisture characteristic curve was obtained (Yao et al., 2014). The nonlinear programming method with minimum relative deviation as the objective function was selected to determine the parameters of the soil moisture characteristic curve model).

gradually adapted to root respiration, which led to an increase in R_s. It is difficult to separate the influence of different factors on R_s throughout the growing season, although we know that looking at either T_s or M_s alone is insufficient for determining R_s (Fekete et al., 2014). Based on this reasoning, the results obtained by the bivariate fitting models of seasonal R_s with T_s and M_s established for the data collected in 2014 and 2015 are considerably more reliable that than those obtained with a single fitting model (Table. 2). Moreover, Zhao et al. (2016) who investigated the effects of aboveground litter on R_s in *Populus davidiana* Dode plantations at different stand ages, obtained the fitting results that are similar to those in our study.

5. Conclusions

As this study of the effect of litter on R_s has shown, the interaction between the quantity and quality of plant litter, T_s, M_s and groundwater leads to the complex diurnal variation of R_s at different stages of the growing season. M_s is the key factor governing changes in the relationship between R_s(CL) and R_s(NL), and the field capacity is an important cut-off point. The coverage of the surface litter has a significant impact on M_s. The balance between the shielding effect of the litter and its decomposition on R_s is not consistent across the entire growing season. Besides, M_s also regulates Q_{10}. The bivariate fitting model of R_s with T_s and M_s achieved higher significant level than R_s established a single fitting model with T_s or M_s. The results of this study suggest that more attention should be paid to negative litter respiration, which may not always be a measurement error. A more in-depth analysis of the precise role played by plant litter in forest ecosystems can also provide useful information that will help us to develop a better understanding of its impact on fragile ecosystems and the terrestrial carbon cycle.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2018.12.005.

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